Acoustic telemetry suggests the lesser spotted dogfish *Scyliorhinus canicula* stays and uses habitats within a French offshore wind farm

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ABSTRACT

Offshore wind farms (OWF) are a rapidly expanding renewable energy source, but their effects on marine wildlife need further investigation. These infrastructures form new artificial habitats that may modify the behaviour and spatial distribution of fish species. Among the species likely to be affected, benthic sharks occupying coastal habitats are particularly exposed to the development of OWF, especially as electrosensitive species. This study used passive acoustic telemetry to investigate the behaviour of a benthic shark, the lesser-spotted dogfish *Scyliorhinus canicula*, within France's first operational OWF. Most tagged sharks remained in the vicinity of the OWF post-release, exhibiting site fidelity and seasonal residency with reduced presence during winter when water temperatures are the lowest. The primary site frequented is a monopile with scour protection on soft substrate, offering potential shelters and food sources. This study provides new insights into the species' ecology and contributes to improving our understanding of how anthropogenic structure installation in the marine environment affects the behaviour of *S. canicula*.

1. Introduction

The use of offshore wind energy has significantly grown in the past decade to address energy transition stakes through decarbonized energy supply (Nabe-Nielsen et al., 2018; Ramos et al., 2021). European countries have emerged as leaders in the deployment of offshore wind farms (OWF) in their waters, largely dominated to date by bottom-fixed installations for which turbines are typically placed on monopile foundations (Esteban et al., 2019; Freeman et al., 2019; Wu et al., 2019). Fixed OWF are usually located in coastal environments at less than 30 km from the shore on soft substrate (Díaz and Soares, 2020). Scour protection is commonly laid out around monopiles to prevent local scour of sediments by wave and current activities, and usually consists of a gravel layer shielded by a rock armour layer (Hammar et al., 2010; Matutano et al., 2013; Wu et al., 2019).

The introduction of these new anthropogenic structures in the ocean generates a multitude of effects on the marine environment, such as an increase in noise emissions mostly during construction phase (Andersson, 2011; Mooney et al., 2020), modified electromagnetic fields around submarine cables (Hutchison et al., 2020) or habitat modifications and associated reef effect (Glarou et al., 2020). It is not entirely clear today how these effects impact ecosystem structure and functioning, which is due, in part, to our limited understanding of species' responses and their subsequent consequences in local ecosystem.

Monopiles and their scour protection are rapidly colonized by invertebrates and crustaceans which generate a change in benthic diversity by increasing the prevalence of hard substrate species leading to modifications in food abundance and trophic relationships (Degraer et al., 2020; Leonhard et al., 2011; Lindeboom et al., 2011; Mavraki et al., 2021). Scour protection may increase seascape complexity through a mosaic of habitats providing new shelters and potential food resource zones for various species (Langhamer, 2012; Raoux et al., 2017). These local habitat modifications can foster an increase in local fish diversity, particularly piscivorous and generalist species (Bergström et al., 2013; De Troch et al., 2013). The presence of soft substrate patches amidst the rocky structures of scour protection can lead to an

increase in the density of fish species associated with soft substrates, such as the European plaice *Pleuronectes platessa,* around monopiles with the diversification of their diets (Buyse et al., 2022, 2023a). Demersal and benthic fish species, such as the Atlantic cod *Gadus morhua*, the common dragonet *Callionymus lyra* and Bullrout *Myoxocephalus scorpius*, are attracted to habitats associated with monopiles as they tend to be present in higher abundance close to the monopiles compared to surrounding areas (Van Hal et al., 2017) and exhibit high degrees of residency (Reubens et al., 2013a, 2013b; Vandendriessche et al., 2013). This attractive effect appears similar to that observed around artificial reefs or fish aggregating devices with a temporary aggregation of mobile species around these anthropic structures (Paxton et al., 2020; Pérez et al., 2020; Wilhelmsson et al., 2006).

To date, studies of fish behavioural responses to OWF presence have primarily focused on commercially important fish species, such as cod *Gadus morhua* (Flávio et al., 2023; Reubens et al., 2013a, 2014), plaice *Pleuronectes platessa* (Buyse et al., 2022) and common sole *Solea solea* (Winter et al., 2010). Yet, other species, such as benthic sharks, may be particularly sensitive to the implantation of OWF, as many of them have a coastal distribution that overlaps with OWF deployment zones (Bergström et al., 2013; Gay, 2012). Benthic sharks rely on their capacity to detect electromagnetic fields for foraging, social interactions, movements and/or migrations (Newton et al., 2019) and the presence of submarine cables within OWFs could have a direct effect on their behaviours (e.g. attraction or repulsion) (Gill et al., 2014; Hutchison et al., 2020). Benthic sharks play a crucial role in the food web by connecting various trophic levels and controlling prey populations (Heithaus et al., 2008). The abundance of fish, molluscs, and crustaceans within OWFs may have an attractive effect on these species, which typically exhibit high fidelity and residency to specific sites (Chapman et al., 2015). This attractiveness could be further enhanced with the presence of scour protection as benthic sharks require reef structures for their reproduction and egg deposition (Katona et al., 2023). In this context, it is important to improve our knowledge of the behaviour of elasmobranchs to assess the effects of OWFs implantation on species with high conservation values (Dulvy et al., 2021; Pacoureau et al., 2021).

Understanding how OWFs impact mobile species' behaviour and habitat occupancy requires adapted approaches for *in situ* monitoring of individuals. Passive acoustic telemetry is one of the methods commonly used to track fish in their environment. Fish are tagged externally or internally with acoustic transmitters that emit a unique identifier at regular time intervals. Their presence is then detected when the tagged fish swims within detection range of acoustic receivers that record timestamped detections and for which the position is known (Hussey et al., 2015). The spatial analysis of these detection data allows to study the species' behaviour at various spatial scales, particularly in terms of habitat preferences, feeding behaviours, residency and movement/migration patterns (Espinoza et al., 2021; Kraft et al., 2023; Lennox et al., 2023). Passive acoustic telemetry has provided insights into the use of artificial reefs by species and their associated behaviour around these structures (Mitamura et al., 2022; Puckeridge et al., 2021). It is often used with elasmobranchs, notably demonstrating site fidelity in certain species such as benthic sharks like Port Jackson sharks *Heterodontus portusjacksoni* (Bass et al., 2021). This approach has already demonstrated its relevance to understanding site fidelity, residency patterns and space use of species within OWF (Buyse et al., 2023b; Reubens et al., 2014).

The lesser-spotted dogfish *Scyliorhinus canicula* is a small benthic shark considered as a model species of elasmobranch (Kimber et al., 2014). This species is commonly found in coastal waters below 19 °C and has an overlapping distribution range with many European OWF (Compagno et al., 2005). It generally uses a wide range of habitats such as sandy, gravelly, and muddy substrates, and is regularly observed around the monopiles within OWFs on European coasts (Ellis et al., 2009; Griffin et al., 2016). *S. canicula* is a generalist opportunistic species that feeds on a wide variety of crustaceans, molluscs, and small

benthic fish (Šantić et al., 2012), including taxa that are highly present around monopiles (e.g. gobiidae, Polybiidae) (Ter Hofstede et al., 2022). Despite observations of this species around OWF monopiles, knowledge on its behaviour and spatiotemporal use of OWFs is still relatively limited. *S. canicula* might adapt its behaviour in response to OWF presence, such as changing its route or adjusting its depth preferences to avoid or use the structures. Alternatively, the species could display aggregation behaviour around OWF areas if they provide favourable conditions.

The present study aimed to investigate the space use and occupancy patterns of *S. canicula* within an OWF off the French Atlantic coastline at three spatial scales using passive acoustic telemetry. We assessed (1) overall residency of *S. canicula* within the OWF, (2) how environmental variables influenced the probability of presence of *S. canicula* according to sex, and (3) occupancy patterns around one monopile equipped with scour protection.

2. Materials and methods

2.1. Study site

This study was conducted at the Saint Nazaire OWF (Fig. 1) located 12 km offshore on the Guérande Bank rocky shelf, north of the Biscay Bay off the Atlantic coast of France (47°09′17.77″ N/02°36′1601″W). Spanning over 78 km², this OWF comprises 80 wind turbines that have been fully operational since November 2022. Wind turbines are installed on monopile foundations, located predominantly on rocky substrates located at 12–25 m deep (Fig. 1; Fig A.1). Patches of coarse substrate found within the OWF are mostly unsteady sandy and gravelly layers laid on bedrock, except for the last line of monopiles in the north-east section of the OWF, which are placed on a depression with dense sediment layers of coarse substrate. These monopiles are equipped with scour protection at their base which consists of stacked rocky blocks (<30 cm wide) extending over a ~20 m diameter and measuring ~2 m in thickness (Fig A.1).

For this study, five different monopiles were monitored (Fig. 1). Monopiles F03, A12 and E12 are located on rocky substrates at 15 m, 22 m and 24 m depth, respectively. Monopile B05 is located on bedrock covered by an unsteady sandy-gravelly layer at 24 m depth. Monopile G06 is located on sandy-gravelly sediment layers at 23 m depth and is surrounded by a 20 m diameter scour protection around the monopile.

2.2. Receiver array

A total of 15 acoustic receivers (TBR 800 release, Thelma Biotel) were deployed within the OWF from May 2022 to June 2023 (Fig. 1). Batches of 3 receivers were placed around each of the 5 monopiles at a distance ranging from 173 to 290 m away from the structure (F03, B05, A12, G06) (Fig. 1). One receiver was lost at monopile E12 early in the study, only data extracted from the 2 remaining receivers were used thereafter. Each receiver was equipped with a sensor set to record sea temperature every 10 min, as well as a synchronisation tag (synch tag) emitting a unique acoustic signal every 10 min (±30 s). Receivers also had an integrated acoustic release system and were deployed using a specifically designed mooring retrieval system which enables to perform the deployment and retrieval of equipment without the need of divers. Deployment occurred in May 2022, while maintenance was conducted in October 2022, February 2023 and the final data were collected in June 2023.

2.3. Range testing and detection performance

The influence of environmental variables on the detection capacity of receivers was analysed using detection data of embedded synch tags. Distance between receivers (of the same monopile) ranged between 350 m and 550 m. For each receiver, detections of synch tags of the two other
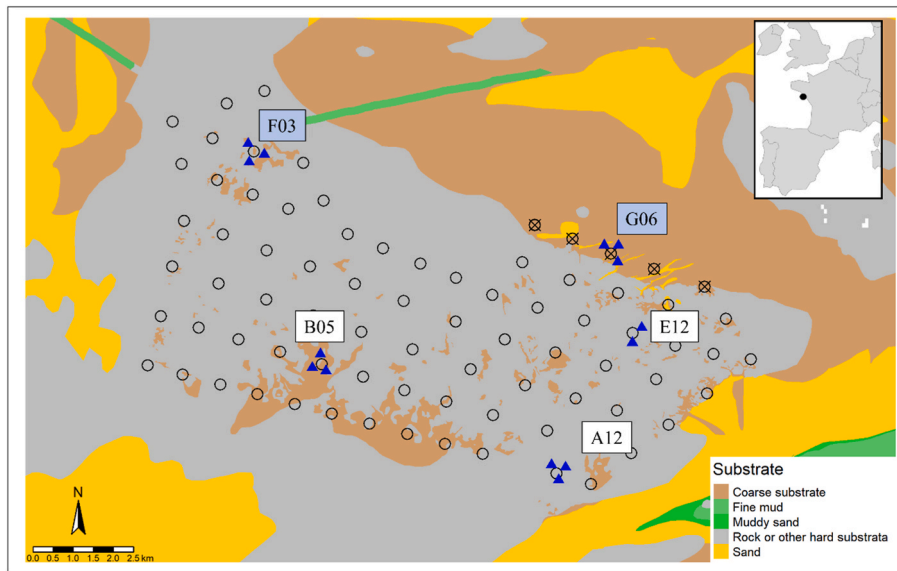
Fig. 1. Map of study site and positions of acoustic receivers within the OWF. Black circles represent monopiles and crossed black circles are monopiles with scour protection. Blue triangles represent receivers, deployed around 5 monopiles. Names of monopiles equipped with receivers are labelled in text boxes with blue-filled boxes indicating monopiles where *S. canicula* were captured and released. The multicoloured background represents the different types of substrates within the OWF indicated in the legend (source: UESeaMap).

receivers associated with the same monopile were extracted. Detection data of synch tags, as well as environmental data were aggregated into hourly bins. Hourly detection probability of a synch tag by a receiver was calculated based on the number of signals received by the receiver divided by the number of signals emitted by the synch tag within 1 h. Detection probability varies from 0 to 1, with 0 indicating no detection during the monitored period and 1 that all emitted synch tag signals were detected by the receiver. Boosted Regression Trees (BRT) were used to examine variation of hourly detection probability in relation to a range of factors (see below for a description of the BRT modelling approach). Distance between receivers, mean hourly wave height and mean hourly receiver tilt were implemented as explanatory variables as these parameters can influence the detection capacity of receivers (Long et al., 2023; Reubens et al., 2019).

2.4. Animal tagging

S. canicula individuals were captured using bottom longlines deployed mostly in the northeast part of the OWF around the monopiles equipped with acoustic receivers (Fig. 1). Preliminary fishing attempts carried out in other sectors of the OWF have not resulted in the capture of individuals. Once aboard the vessel, individuals were placed into an oxygenated water tank to recover from capture. Each individual then underwent a general anaesthesia procedure using benzocaine at a concentration of 50–60 mg/l. General anaesthesia was maintained for all subsequent operations by intubating individuals with 40 mg/L benzocaine sedation. The sex, fork length (in cm) and total length (in cm) of each individual were recorded. An acoustic tag (Thelma Biotel ID-2MP13, 69 kHz OPi, 90–150 s ping delay) was inserted into the intraperitoneal cavity of the shark by surgery. The incision was closed using 2 to 3 stitches of sterile and absorbable monofilament sutures (size 2) with a reverse triangular needle (VICRYL Plus; Ethicon Inc., Somerville, NJ). To facilitate reporting by fishermen in case of recapture, individuals were externally tagged using a Peterson disc of 1 cm diameter attached to the first dorsal fin on which was inscribed a unique ID number and contact information. Following tagging procedures, individuals were placed in an aerated water tank for ~20 min (until full motile recovery) and subsequently released near the capture location. Ethical guidelines were strictly observed, and tagging was carried out under a project

licence no #35806–2022030910351678 authorized by the French Ministry of Agriculture and Environment.

2.5. Data analysis

Raw detection data were uploaded to the secure European Tracking Network (ETN) platform which centralises acoustic telemetry data at European scale (Reubens et al., 2018). Detection data used for analysis were extracted from the ETN database. All data processing and statistical analyses were conducted under R version 4.1.2 (R Core Team, 2021). Detection data were filtered to remove potential false detections. Acoustic signals detected only once in a day were removed and unlikely detections were removed based on realistic time intervals between detections, considering distances and elapsed time (Daly et al., 2014; Meyer et al., 2007). To mitigate potential behavioural biases from capture and tagging trauma, acoustic detections occurring within 48 h after the individual release were excluded from the analysis (Murray et al., 2015).

2.5.1. Residency of individuals within the OWF

Detection data from all receivers were binned into daily presence with an individual considered to be present when at least two detections were recorded within 24 h. For each individual, the overall residence index (RI) within the OWF was calculated by dividing the number of days the individual was detected by the total number of days it was monitored (Appert et al., 2023). The RI ranges from 0 to 1, with 0 indicating the absence of the individual over its monitored period and 1 indicating that the individual was present every day of its monitored period. For each individual, the RI was calculated monthly. Mean monthly RI ($\pm$ standard error - SE) were calculated for males and females to examine seasonal variation in gender presence within the OWF. Non-parametric Kruskal-Wallis tests were used to assess differences in RI among months for each sex, with a significant level of $p < 0.05$. In cases where the Kruskal-Wallis test indicated a significant difference, post-hoc pairwise comparisons were performed using the Conover-Iman test, with p-values adjusted using the Benjamini-Hochberg method using the 'conover.test' package (Dinno and Dinno, 2017).

2.5.2. Occupancy patterns within the OWF

For each monitored monopile, detection data of all receivers were combined and the total number of detections per monopile was calculated for each individual. Bipartite graphs were produced to link individuals to the monopiles they visited using the 'igraph' package (Csardi, 2013). These 'bipartite' networks consist in two types of nodes (Dale and Fortin, 2010): (i) individuals and (ii) monopiles. The centrality of each monopile node was calculated using node strength (weighted degree), which represents the sum of associations between individuals and each monopile. All individuals are connected to each monopile by an edge for which thickness is weighted by the logarithm of the detection number for the monopile. Graphs were generated using the Kamada-Kawai layout algorithm (Kamada and Kawai, 1989). This algorithm minimises the distance between nodes while matching the ideal representative length of their connections (Boulouard et al., 2017). Individuals were separated into two groups according to their capture/release zone. Networks were generated for individuals captured/released around F03 and for individuals captured/released around monopile G06 (Fig. 1). A 'bipartite' network was produced for each group to examine connectivity amongst monitored monopiles based on the capture/release zone.

BRT were used to investigate the influence of environmental and anthropogenic factors on *S. canicula* probability of presence around each monopile within the OWF. This modelling approach is considered a powerful technique for assessing the distribution of fish (França and Cabral, 2015) as (i) it is insensitive to the multicollinearity of variables and outliers, (ii) it identifies the influence of predictor variables on the probability of presence and (iii) detects potential thresholds of these variables (Dedman et al., 2017; Elith et al., 2008; Valavi et al., 2022). More details on this method can be found in Elith et al. (2008). For each monopile, detection data were grouped into 1-h bins. The probability of the presence of *S. canicula* was calculated hourly with the number of individuals present at the monopile divided by the total number of individuals present within the OWF at the same hour. To examine the difference between sexes in the presence probability, BRT models were implemented for each sex. BRT models were applied using the 'gbm' (Ridgeway et al., 2013) and 'dismo' (Hijmans et al., 2017) packages. The learning rate and tree complexity are two key parameters to adjust BRTs (Elith et al., 2008). Different values of these parameters were tested (tree complexity: 2,3; learning rate: 0.1, 0.05, 0.01, 0.005, 0.001, 0.0005 and 0.0001). Model performance was evaluated based on cross-validation (CV) score, the area under the curve (AUC), which is a measure of the model's performance with a value between 0 and 1 and the training AUC which is an estimate of the model's performance on several subsets of data, based on cross-validation. The best model was selected based on these parameters, particularly by the lowest CV value and the maximum AUC value. If the difference between the AUC and the training AUC is important, this may indicate that the model has been over-fitted to the data. A comparison of the contribution of explanatory variables on the probability of the presence of male and female *S. canicula* was conducted using the 'ggBRT' package (Jouffray et al., 2019). The relative contribution of each variable in each BRT model was measured using the percentage of tree splits attributed to that variable and plots of the fitted function were generated from the model's results and used to illustrate relationships between the probability of the presence of *S. canicula* and each explanatory variable with a contribution >10% indicating a significant effect (Elith et al., 2008).

2.5.3. Explanatory variables

Several explanatory variables were added to analyse their relationships with the probability of the presence of *S. canicula* (Table 1).

The substrate type is likely to explain occupancy patterns as *S. canicula* can use a wide range of habitats (Papadopoulo et al., 2023; Sims, 2003; Wearmouth et al., 2012). The substrate type associated to each monitored monopile was included as a categorical variable with 3 levels: Coarse substrate with scour protection for the G06 monopile, coarse

Table 1
Summary of variables used in the Boosted Regression Tree models.

Explanatory variable	Type	Description	Values/units
Sea temperature	Continuous	mean hourly temperature	Degrees Celsius (°C)
Current speed	Continuous	mean hourly current speed	Meters per second (m/s)
Time of day	Categorical	time of day period	Sunrise, day, sunset, night
Moon phase	Categorical	moon phase categorised based on moon illumination data	New, Waxing, Full, Waning
Substrate type	Categorical	Substrate associated with the monopile	Rocky, coarse substrate patch, coarse substrate with scour protection
Other sex presence	Categorical	Presence or absence of the other sex within the same hour	1: Presence/0: Absence
Tide	Categorical	Tidal phase	Low, flood, high, ebb
Rotor speed	Continuous	Mean hourly rotor speed	Number of rotations per minutes
Wave height	Continuous	Mean hourly wave height	Meters

substrate patch for the B05 monopile and rocky substrate for the A12, E12 and F03 monopiles.

The time of day can influence the behaviour of *S. canicula* as the species tends to be active mostly at night (Papadopoulo et al., 2023). *Time of day* was included as a categorical variable with 4 levels: day, night, sunset, sunrise. Sunrise and sunset correspond to a 2h period of ±1 h around the sunrise and sunset time and were extracted using the 'photobiology' package (Aphalo, 2016).

The sea temperature affects the distribution of *S. canicula*, with the individuals' probability of presence increasing with temperature up to 16.6 °C and decreasing beyond (Papadopoulo et al., 2023). The mean hourly *sea temperature* (degrees Celsius) near the seabed recorded by the receivers was added as a continuous variable.

The moon phase can influence the behaviour of benthic elasmobranchs with a change in depth and vertical activity (Hammerschlag et al., 2017). *Moon phase* was added as a 4-level categorical variable based on illumination intensities (New, Waxing, Full, Waning) extracted from the 'lunar' package (Lazaridis, 2022).

Tide and current speed can affect the locomotion and presence of some elasmobranch species (DiGiacomo et al., 2020; Murie et al., 2023). *Tide and current speed* data were obtained from the E.U. Copernicus Marine Service Information in a 1.5 km² resolution block centred on each monopile (https://www.copernicus.eu/en). Modelled data were extracted on a 30-mintue interval and used to calculate an hourly mean.

Wave height can affect the presence of some benthic sharks, such as the zebra shark *Stegostoma fasciatum* which are less likely to be present with increasing wave height (>1.5m) (Dudgeon et al., 2013). *Wave height* was provided by the society Parc du Banc de Guérande, regrouping the developers of the OWF, from data collected using an instrumented buoy deployed near to the substation at the centre of the OWF (47°09′17.64″ N/02°36′17.4″W). Data logged every 10 min were used to calculate hourly means.

Other sex presence: to account for potential sex spatial segregation of *S. canicula* (Kimber et al., 2009), the hourly presence or absence (1 or 0) of the opposite sex was added as a categorical variable if at least one individual of a different sex is detected at the same time.

Rotor activity of the turbine can produce vibrations that travel through the monopile and emit underwater noise (Nabe-Nielsen et al., 2018; Zhang et al., 2021). *S. canicula* tends to avoid areas with important anthropogenic noise (de Vincenzi et al., 2021). The turbine rotation speed of each monopile over time, measured in rotations per minute, was provided by the society Parc du Banc de Guérande. Data were used to calculate hourly means.

2.5.4. Time presence around scour protection monopile

Monopile G06, the only monitored monopile equipped with scour protection, had the highest number of detections. Continuous resident time (CRT) metrics were calculated to illustrate the importance of the monopile G06 within the OWF (Capello et al., 2015). Only individuals with a RI > 0.1 were selected for this analysis. This method was used to produce continuous time sequences at a specified temporal scale for each individual. A sequence was deemed to have terminated if no detection of the individual occurred for a period of ≥10 min (corresponds to a mean of 5 signals) (Capello et al., 2015). CRTs were computed at the OWF-scale for each individual, considering detections combined from all monopiles. CRTs were also computed at monopile G06-scale for each individual by only considering detections from receivers deployed around this structure. The percentage of time spent around to the monopile G06 in relation to the time spent in the OWF area for each individual was then calculated.

We examined grouped detection data from G06 receivers to analyse the presence around this monopile according to the hour of day. The frequency of detections for each individual was calculated hourly. A Generalized Linear Mixed Model (GLMM) (family = Gaussian, link =

Table 2

Summary of the metadata and residency index (RI) for the tagged individuals *S. canicula* at St Nazaire OWF.

Tag ID	Sex	Total length (cm)	Weight (g)	Capture/ release monopile location	Release date	Last detected	No. of days detected	No. of detections	RI
OPI-761	M	67	1100	G06	24/08/2022	01/03/2023	61	13249	0.196
OPI-763	F	61.5	1100	F03	25/08/2022	27/06/2023	12	360	0.039
OPI-765	F	63	1200	F03	25/08/2022	07/11/2022	7	28	0.023
OPI-766	M	61	1000	F03	25/08/2022	16/12/2022	4	141	0.013
OPI-767	F	61	980	G06	25/08/2022	26/08/2022	2	432	0.006
OPI-768	F	65	1005	G06	25/08/2022	16/05/2023	15	342	0.048
OPI-769	F	66	1005	G06	25/08/2022	22/01/2023	97	8568	0.313
OPI-770	M	61.5	860	G06	25/08/2022	13/04/2023	14	4296	0.045
OPI-771	M	61	700	G06	25/08/2022	18/03/2023	13	2189	0.042
OPI-772	M	61.5	830	G06	25/08/2022	29/06/2023	133	45759	0.429
OPI-773	M	62	720	G06	21/09/2022	18/10/2022	21	3283	0.074
OPI-774	F	64	1100	G06	21/09/2022	07/06/2023	71	4308	0.251
OPI-775	M	63	875	G06	21/09/2022	21/03/2023	24	856	0.085
OPI-776	F	61	790	G06	21/09/2022	21/09/2022	1	295	0.004
OPI-777	F	59	845	G06	21/09/2022	17/11/2022	2	79	0.007
OPI-778	M	61	730	G06	21/09/2022	27/09/2022	7	1051	0.025
OPI-779	M	59	810	G06	21/09/2022	19/10/2022	26	8030	0.092
OPI-780	M	61	740	G06	21/09/2022	29/06/2023	82	8171	0.29
OPI-781	M	60	720	G06	21/09/2022	26/10/2022	2	244	0.007
OPI-782	M	66	1010	G06	22/09/2022	20/04/2023	18	739	0.064
OPI-783	M	64	1090	G06	22/09/2022	29/06/2023	65	11167	0.23
OPI-784	M	63	800	G06	22/09/2022	01/11/2022	9	909	0.032
OPI-785	M	62	780	G06	22/09/2022	28/06/2023	82	7400	0.291
OPI-786	M	60	690	G06	22/09/2022	25/01/2023	27	2132	0.096
OPI-787	M	65	950	G06	22/09/2022	29/06/2023	113	12112	0.401
OPI-790	F	66	1200	G06	05/10/2022	28/10/2022	4	165	0.015
OPI-791	F	63	1020	G06	05/10/2022	21/11/2022	8	268	0.03
OPI-792	F	64	1160	G06	05/10/2022	28/06/2023	71	3945	0.264
OPI-794	F	66	1100	F03	18/10/2022	24/06/2023	29	838	0.113
OPI-795	F	64	1120	F03	18/10/2022	08/06/2023	44	3639	0.172
OPI-796	F	65	1100	F03	18/10/2022	26/01/2023	13	90	0.051

log) was implemented using the 'lme4′ package (Bates et al., 2009) to examine the effect of hour of day and sex on individual frequency of detections. Detection frequency was included as a response variable, the interaction between hour of the day and sex as a fixed explanatory variable, and the individual as a random factor. The hour of day was fitted with a harmonic polynomial to ensure continuity between beginning and end of the days' signals. Predicted values of detection frequency from the best-fit model were visualized using the 'ggplot2' package (Wickham et al., 2016).

3. Results

A total of 31 *S. canicula* individuals were tagged with an acoustic transmitter within the OWF, between August 2022, and October 2022, comprising 17 males and 14 females (Table 2). All tagged individuals were detected at least once within the study site. In total, 143,357 detections were recorded over 309 days from August 2022 to June 2023 (a total of 129,188 detections were considered in this study after applying data filtering).

3.1. Range testing and detection performance

The BRT model used to evaluate range testing performed well, with an AUC of 0.92 (Table A.1). Range testing results revealed variability in the detection distance, with a high detection probability between 350 and 450 m, rapidly dropping beyond 450m. The second most influential variable was *wave height* with a significant negative effect on detection probability above 4-m wave height. Detailed results are presented in the supplementary information (ig A.2, Table A.1).

3.2. Residency of individuals within the OWF

The number of days of presence varied among individuals from 1 day to 133 days (mean: 34.7 ± 36.8 SD; median = 18) and the number of detections per individual from 28 to 45,759 detections (mean: 4680.161 ± 8586.386 SD; median = 1051) (Table 2). The overall RI of *S. canicula* across all monitored monopiles present a mean of $0.12 \pm$ SE 0.02 with values ranging from 0.004 to 0.43 (Table 2).

The daily individual detection around the monitored monopiles within the OWF showed inter-individual variations (Fig. 2). In total, 33% of tagged individuals, 6 females and 4 males, were present for less than 10 days within the array, of which 25% disappeared a few weeks after tagging (i.e., female OPI-767; male OPI-781) (Table 2; Fig. 2).

Overall, 33% of individuals showed a RI > 0.1 (11 individuals: 6 males; 5 females) (Table 2). Although 1 individual was present throughout the monitoring period (OPI-787; RI = 0.4), presence of males generally showed a seasonal trend (Fig. 2). Overall, males were detected within the array from August to December, then absent from December to March (winter) and detected again from March to June (spring) (OPI-772; OPI-780; OPI-783; OPI-785) (Fig. 2). The mean monthly RI for males was the lowest in winter from December (RI = 0.03; SE $\pm$ 0.08) to March (RI = 0.05; SE $\pm$ 0.02) with a significant difference between these winter months and the first 3 months of the study (p.value < 0.05) (Fig. 3; Table A.2). The highest RI values were in the first 3 months of the study in summer/autumn (e.g., September 2022 RI = 0.45; SE $\pm$ 0.08) and at the end of the study in June 2023 in spring (RI = 0.24; SE $\pm$ 0.09) (Fig. 3). This seasonal trend was also observed for females but over a shorter period with an absence of individuals from January to March 2023 (winter) except for two individuals (Fig. 2). These two females showed a regular presence within the array throughout the study (OPI-792 RI = 0.26; OPI-794 RI = 0.11). August month showed significantly higher RI compared to all other months for both sexes, however, RI was only calculated for 4-day-monitoring within that month. The mean RI for females did not show a significant difference among months (except for August) but, as for males, the highest mean RI values were in the first 3 months of the study (e.g., September 2022 RI = 0.26; SE $\pm$ 0.15) and decreased sharply in the winter months with a minimum RI of 0.08 (SE $\pm$ 0.03) in December 2022 (Fig. 3; Table A.3).

Last detected corresponds to the last day the individual was detected within the OWF. *Capture/release monopile location* is the area around the monopile where the individual was caught and released. *Number of days detected* is the number of days the individual was detected at least two times. *No. of days detected*, *No. of detections* and *Residency Index* were calculated without removing the 48h after release.

3.3. Occupancy patterns within the offshore wind farm

Overall, the majority of tagged individuals were captured and released around monopile G06 and only 6 individuals were captured and released around F03 (Fig. 1; Table 2; Fig. 4). The bipartite network revealed a relatively heterogeneous use within the OWF among individuals and monopiles. Monopile G06 consistently ranked as the most central monopile node in the bipartite networks for the two release monopiles. The associated strengths from the networks for G06 were 182.1 for individuals captured and released around this monopile and 28.6 for individuals captured and released around F03 (Fig. 4,
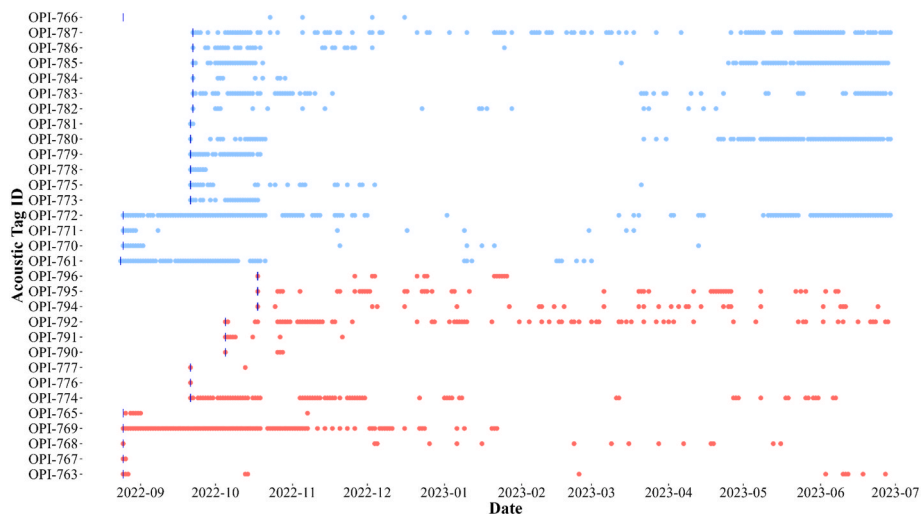

Fig. 2. Daily individual detection around the receiver-equipped monopiles within the OWF for 31 individuals. Daily presence was calculated without removing the 48h after release. Blue dots represent males; red dots represent females. Blue dashes represent the date of capture and release of individuals.
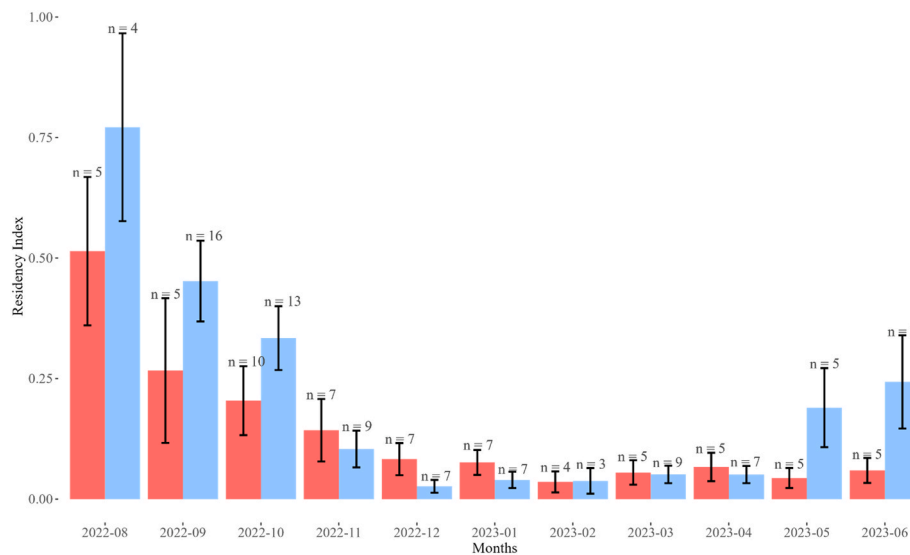
Fig. 3. Mean monthly residency index of individuals around monopiles equipped with receivers with standard errors. Blue barplots represent males (n = 16); red barplots represent females (n = 12). *n* represents the number of individuals per month for males and females present in the array.

Table A.4). In comparison, the other monopile nodes had a mean strength of 17.5 (SE ± 0.8) for individuals captured and released around G06 and a mean strength of 7.3 (SE ± 5.8) for individuals captured and released around F03 (Fig. 4, Table A.4). This indicates that monopile G06 was visited by the highest number of individuals and is the most central monopile in the networks (Fig. 4).

The bipartite network of individuals captured/released near monopile F03 showed a spatial preference for monopile G06 (strength: 28.6 for G06; 14.1 for F03), with all individuals detected around G06 and an average of 71% (±41.6%) of detections on this monopile located 9.2 km from F03 (Fig. 4). The connection for individual OPI-795 was relatively high for monopile G06, with 97% of detections made at this monopile. Monopile G06 was the main node for all individuals captured and released around this monopile with a strength of 182.1 (Fig. 4, Table A.4). Among these individuals, 10 (5 males and 5 females) were exclusively detected around monopile G06; 7 individuals (6 males and 1 female) visited monopile F03 and 4 individuals (2 males and 2 females) visited the B05 monopile, located 7.8 km from monopile G06 (Fig. 4). Overall, for individuals captured and released around G06 or F03, bipartite networks showed that individuals moved among monopiles but in a limited way and with a strong presence around monopile G06 even for individuals captured and released 9.2 km away (Fig. 4).

Several BRT models have been developed to evaluate the effect of different variables on the probability of presence of males and females within the OWF. Among all models tested, the best-fit BRT model for both males and females included the parameters with a tree complexity of 3 and a learning rate of 0.05 (Table 3; Table A.5). For males, the CV of 0.14 and the AUC value of 0.99 indicated a robust performance of the model, and the small difference with the training AUC value (0.98) indicated that the model was no overfitted (Table 3). For females, the model was also robust with a CV of 0.17, an AUC of 0.96 and a training AUC of 0.94 and a slight overfitting of the model.

For both models, *Substrate* was the most influential variable for both sexes, accounting for 45.7% for males and 40.4% for females (Fig. 5). Coarse substrate with scour protection had a positive effect on the probability of *S. canicula* presence in both models, while other substrates had a negative effect. The second most significant variable was *Sea temperature*, contributing 22.6% for females and 33.7% for males. Mean sea temperature exhibited a positive increasing effect for both males and females, peaking around 16 °C before declining. *Wave height* ranked third, contributing 12% for males and 10.2% for females and mean wave height had a negative effect on presence beyond 3 m for both models.

Other variables exhibited minimal influence on the probability of *S. canicula* presence around monopiles, each contributing less than 10%.

Summary of starting parameters (Learning rate, Tree complexity and Bag fraction) and performance metrics (Number of trees, Training AUC, AUC = area under the curve and Cross-validation score, with SE in parentheses) for the best-fit boosted regression tree models of *S. canicula* presence for males and females.

3.4. Presence around monopile G06 with scour protection

Individuals with a RI > 0.1 exhibited CRTs ranging from 20 to 1533 h (mean = 353 h ±410 SD; median = 293) across all monitored monopiles (Table 4). CRTs calculated for monopile G06 were more variable among individuals, with CRTs ranging from 8 to 1529 h (mean = 345 h ±411 SD; median = 293 h). The percentage of CRT close to monopile G06 showed little inter-individual and inter-sex variability, ranging from 40,5%–100% (mean = 91,8% ± 18,1) (Table 4).

The detection frequency of *S. canicula* around to monopile G06 was significantly influenced by the interaction of time of day and sex (GLMM, p.value < 2.63e-6), with different patterns observed for males and females (Fig. 6; Table 5). Females exhibited a higher detection frequency around the monopile during nighttime (from 7:00 p.m. to 7:00 a.m.) (Fig. 6; Table 5). Detection frequency around monopile G06 for males was more homogeneous according to the hour of day and between day and nighttime (Fig. 6).

4. Discussion

This study used passive acoustic telemetry to investigate the influence of environmental factors on the presence of *S. canicula* within France's first operational OWF equipped with monopile foundations. Based on 14 females and 17 males tagged, results show that most sharks remained in the vicinity of the OWF after release. With almost a year of tracking, this study indicate that presence of the species is seasonal, with a more noticeable pattern for males than for females. Individuals were mostly detected in the area where most of them were caught and released, suggesting that *S. canicula* shows high site fidelity. The main site frequented is a monopile installed on soft substrate and equipped with scour protection, where individuals may find shelters to rest and food to eat or reduce opposite-sex interactions. This study provides new insights into the species' ecology and contributes to improving our understanding on how anthropogenic structure installations in the marine
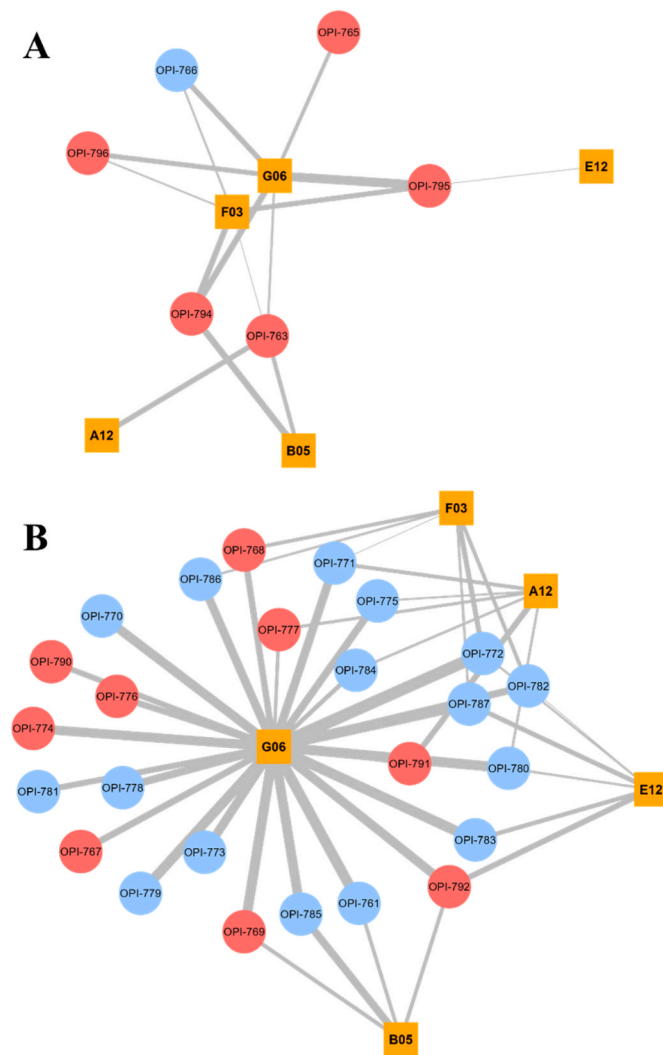
A

B

Fig. 4. Bipartite networks of *S. canicula* individuals according to their capture/release monopile. Bipartite networks of *S. canicula* individuals (circular nodes; blue = males; red = females) linked to monopiles (square nodes) based on the log of the number of detections separated according to their capture/release monopile (A: Individuals captured and released around monopile F03 (n = 6); B: Individuals captured and released around monopile G06 (n = 25)). Graphs were generated using the Kamada-Kawai layout algorithm.

environment affect the behaviour of *S. canicula*.

4.1. Residency and seasonal occurrence of S. canicula within the OWF

Scyliorhinus canicula uses coastal habitats with a distribution that overlaps with OWF development zones in all EU waters (Elliott et al., 2020). The species has been previously observed within OWF in the Irish Sea and the North Sea (Griffin et al., 2016). However, knowledge on occupancy patterns and space use in these anthropogenic habitats remains scarce. Our study showed that most tagged individuals of *S. canicula* displayed some degree of residency to the OWF area with RI of up to 0.43 and with some individuals being detected up to 133 days

after release. Papadopoulo et al. (2023) showed similar patterns for this species in a Spanish marine protected area where over 24% of tagged individuals had high residency index (RI > 0.5) to natural habitats. This suggests that the presence of the OWF does not, at least within our monitored areas, hinder *S. canicula* presence.

Sea temperature strongly influenced the presence of *S. canicula* within the OWF with individuals favouring waters around 16 °C which is in line with findings conducted off western Spain and in the Bay of Biscay on this species (Papadopoulo et al., 2023; Rodríguez-Cabello et al., 2007). Although the number of data points in our study above 16 °C remained limited, the sharp decrease in occurrence revealed by our best-fit model fits with observations from Sims et al. (2006), that *S. canicula* tend to avoid water above 16 °C. The progressive increase in occurrence with rising sea temperatures for both males and females suggests a thermal niche between 11 °C and 16 °C for *S. canicula*. This species tends to move toward warmer waters during winter (Papadopoulo et al., 2023) which likely explains the low presence of individuals at our study site when waters reached temperatures below 11 °C. Overall, the seasonal trend of *S. canicula* presence observed in our study is comparable to current knowledge on the species.

Several individuals displayed some degree of site fidelity to monopiles as they were detected at the same site several times but with periods of absence of several weeks. Site fidelity to OWF areas has already been demonstrated for several fish species and has been linked to foraging (Buyse et al., 2023b; Gimpel et al., 2023; Reubens et al., 2013c). Similarly, benthic sharks usually display site fidelity to specific habitats, often driven by reproductive or foraging needs (Bass et al., 2021; Chapman et al., 2015). The high RI of both male and female *S. canicula* individuals as well as the return of individuals after long absences suggest that the St Nazaire OWF offers suitable habitats outside winter where *S. canicula* may fulfil biological functions such as feeding and reproducing. Direct observations of gravid females during tagging sessions in early summer indicate that the OWF area may also be used as a spawning site by the species (L. Couturier unpublished data).

The main limit of acoustic telemetry is that when an individual is not detected, it is not possible to know whether it has left the area or whether it is present but outside the detection range of receivers. Our study design only allowed for a small area of the OWF to be monitored (≈4 km^2 spread over 5 monopiles spaced several kilometres apart). As such, the observed residency index of *S canicula* within the OWF is likely to be underestimated. A denser network of receivers covering a larger surface would provide a deeper understanding on the residency and movements of *S. canicula* within the OWF.

4.2. Distribution of S. canicula within the OWF

Scyliorhinus canicula is commonly associated to soft substrates (Sims, 2003; Wearmouth et al., 2012). This was also observed in our study as both males and females mostly occupied the area around the monopile installed on coarse substrate and equipped with scour protection. This trend is likely to be influenced by the fact that individuals were mostly caught and released around this area. All individuals were present at some point in the vicinity of the monopile. Some individuals had a near continuous presence within receivers' detection range, staying continuously up to 133 days. Other individuals travelled within the OWF and occupied, to some extent, areas around monopiles installed on rocky substrate. Our results did not show any diurnal effect on the presence of *S. canicula* at the OWF scale but indicated higher nighttime occupancy for females around monopile G06. Ecological knowledge of the species

Table 3
Summary of parameters for the best-fit boosted regression tree model.

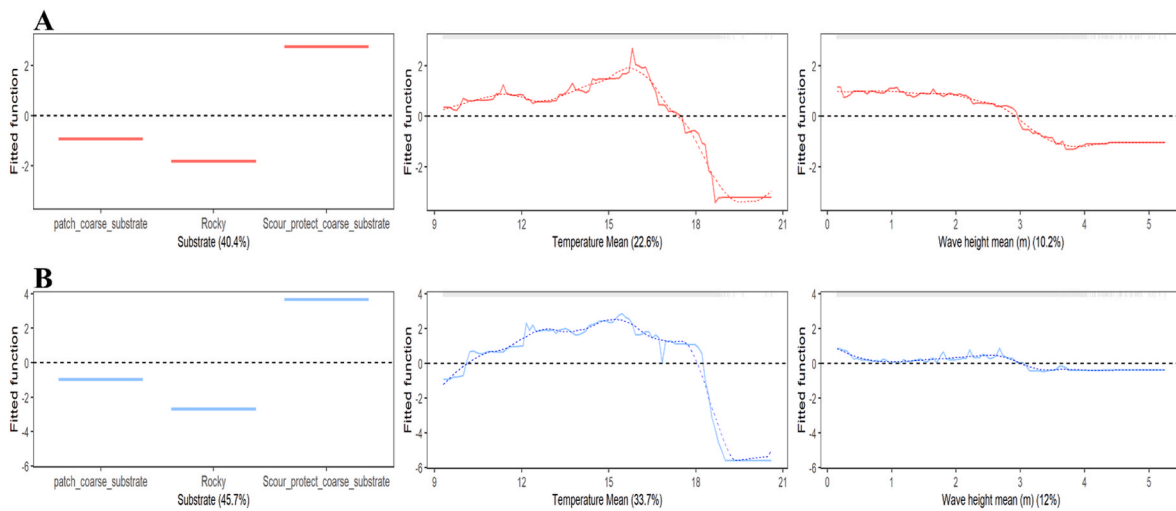| Model	Learning rate	Tree complexity	Bag fraction	Number of trees	Training AUC	AUC	Cross validation score (SE)
Males	0.05	3	0.7	3200	0.983	0.993	0.14 (0.001)
Females	0.05	3	0.7	2050	0.943	0.969	0.17 (0.003)

Fig. 5. Marginal effect plots of the most influential environmental variables with a relative contribution > 10% into the likelihood of *S. canicula* presence from Boosted Regression Trees models, for (A) 12 females and (B) 16 males. Red (A) blue (B) dashed lines represent the smoothed function of the variables. Black dotted lines represent the value 0; the delineation between the positive or negative effect of values.

Table 4
Summary of individual information at two spatial scales (overall OWF and monopile G06) for individuals with a residency index > 0.1 (6 males and 5 females). RI = residency index, CRT = continuous residency time.

Acoustic tag ID	Sex	Monopile Captured/ Released	No. of days detected	RI	Total CRT within the OWF in the array (hour)	Total CRT around the G06 monopile (hour)	% of time around the G06 monopile
				OWF scale		G06 monopile scale	
OPI-761	M	G06	61	0.196	350.3	349.5	99.8%
OPI-769	F	G06	97	0.313	301.7	300.2	99.5%
OPI-772	M	G06	133	0.429	1533.3	1529.7	99.8%
OPI-774	F	G06	71	0.251	151.0	151.0	100.0%
OPI-780	M	G06	82	0.29	306.9	305.9	99.7%
OPI-783	M	G06	65	0.23	293.2	293.2	100.0%
OPI-785	M	G06	82	0.291	259.9	205.7	79.2%
OPI-787	M	G06	113	0.401	438.2	432.6	98.7%
OPI-792	F	G06	71	0.264	125.7	116.7	92.8%
OPI-794	F	F03	29	0.113	20.0	8.1	40.5%
OPI-795	F	F03	44	0.172	105.6	105.4	99.8%

OWF scale with the number of days detected and Residence Index and total continuous time within the array in the OWF based on CRTs. G06 monopile scale with total continuous time around this monopile based on CRTs and the percentage of time around the monopile representing the total time around the monopile divided by the total time in the OWF area as a percentage.
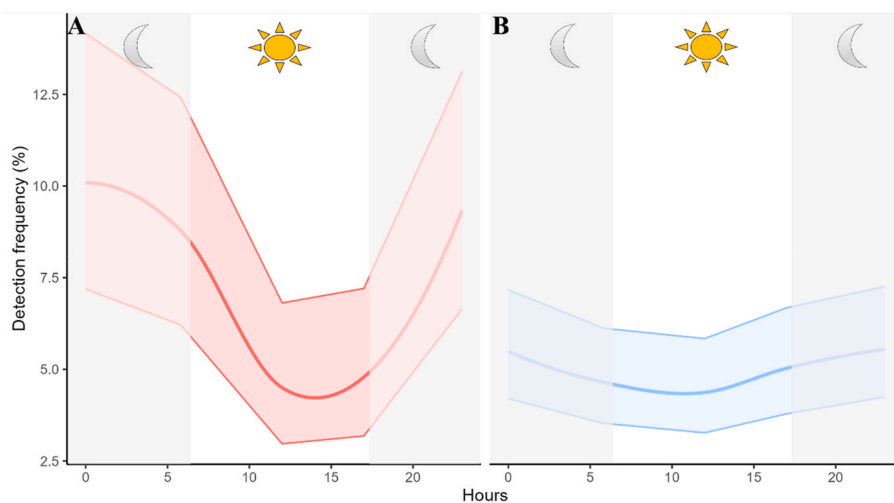

Fig. 6. Predicted values of detection frequency from the best-fit generalized linear mixed effects model for variables sex and hours of the day (A: females; B: Males). The y-axis has a range of values and designates a relative scale of the detection frequency for each sex.

Table 5

Output of the GLMM model fitting detection frequency by time of the day and sex.

Fixed variables	Estimate	Standard error	t-value	Pr(>|z|)	
(Intercept)	1.90744	0.17260	11.051	<2e-16	***
harm(Hour)c1	0.40400	0.08600	4.698	2.63e-06	***
harm(Hour)s1	0.24477	0.07707	3.176	0.00149	**
Sex Males	−0.31905	0.21362	−1.493	0.13531	
harm(Hour)c1:Sex Males	−0.28997	0.10818	−2.681	0.00735	**
harm(Hour)s1:Sex Males	−0.30283	0.10101	−2.998	0.00272	**

Output of the model with significant effect of variables sex and hours of the day in comparison to the intercept (Frequency of detections). Intercept includes Sex – Hour of the day with a harmonic polynomial (harm). Significant codes: '***'0.001, '**' 0.01, '*' 0.05; Freq ~ harm (Hour) * Sex + (1 | Tag.ID).

indicates that *S. canicula* is mostly active at nighttime to foraging while resting close to the sea bottom during the day (Munroe et al., 2022; Papastamatiou and Lowe, 2012; Šantić et al., 2012; Sims et al., 2006). The lack of clear diurnal trend across the OWF in our study may indicate that the species uses the area for both resting and feeding.

Scyliorhinus canicula displays sex segregation in space use as females seek refuge and aggregate in crevices to avoid sexual harassment and unsolicited mating from males (Rodríguez-Cabello et al., 2007). Our study did not detect any sexual segregation in occupancy patterns within the OWF. Both male and female individuals present their highest occurrence rate near the monopile equipped with scour protection. The rock armour may provide small shelters used as hiding places for females while males occupy the surrounding area and which might explain that both sexes seem to share this same habitat, but they are not active at the same time of the day. On the other hand, our study design does not allow for the calculation of fine-scale positioning of individuals within the monitored area and the range testing of receivers indicates a detection area around monopile of $\approx 1{,}2$ km^2 which limits our capacity to thoroughly investigate spatial sex segregation.

Despite the potential influence of numerous abiotic factors on the presence and behaviour of elasmobranchs (Schlaff et al., 2014), our models did not show strong relationships between the majority of tested environmental variables and the presence of *S. canicula* within the OWF. Wave height had a strong influence on *S. canicula* presence within the OWF. Turbulences induced by wave height and frequency can influence the presence and activities of benthic sharks in exposed areas, especially in shallow waters (e.g. Dudgeon et al., 2013). Waves reaching over 4 m height can generate motion in waters less than 20 m depth (Leonhard et al., 2011). St Nazaire OWF has a mean depth of ≈ 19 m where waves above 4 m height may induce disturbances near the seabed that affect *S. canicula.* The species may either hide deep into rocky crevices, which prevents the acoustic signal of their tags to be picked up by receivers, or leave the area toward deeper waters during strong weather events. However, wave height was also the most important factor explaining reduction in receivers' detection capacity, it is thus possible that sharks were present in the area even during these events but not detected by receivers due to high ambient noise (Reubens et al., 2019).

Our study did not reveal any significant effect of time of day, lunar phases, water height, and current speed on the presence of *S. canicula* at the scale of the whole OWF. These results indicate that tidal intensity, which can generate strong currents, may not influence habitat use of *S. canicula* in this area, although accuracy of current data used in our models may be limited by the resolution obtained from Copernicus platform (Den Boon et al., 2004). *Scyliorhinus canicula* usually changes its activity patterns between day and night (Papadopoulo et al., 2023; Sims et al., 2001). The trend was only observed in this study for females at the scale of monopile G06. Artificial nighttime illumination produced by OWF could contribute to changes in activity patterns and explain the

lack of diurnal trend, particularly for males. To meet maritime navigation regulations, each monopile must be equipped with white lights illuminating the mast so that the structure is visible at a 360° angle (regulations for France can be found in Decree of April 23, 2018 and the technical note of 11/07/16 'relative aux mesures de sécurité maritime applicables à la planification d'un champ éolien en mer'). This light source, directly projected toward the water, may reach the sea bottom and influence *S. canicula* behaviour, although, to our knowledge, this pressure is yet to be quantified.

The rotation of wind turbines can generate vibrations and underwater noise (Zhang et al., 2021) that may affect *S. canicula* behaviour as the species tends to flee an area when exposed to anthropogenic noise (de Vincenzi et al., 2021). Yet, our study did not reveal any relationship between the rotation speed of the turbine rotor and the species presence. Although the ambient noise was not recorded for this study, it is possible that the intensity and frequency of acoustic emissions generated by the turbine's activity are either not perceived by *S. canicula* or the disturbance level is offset by other habitat characteristics making the area still suitable for the species. A study design that involves a dense receiver network would enable a triangulation approach to accurately determine the position of individuals in space and time. This would allow us to assess whether individuals tend to distance themselves from the monopile when turbines are operating at high speeds.

4.3. Monopiles with scour protections as interesting habitat

All individuals used at some point the area around the monopile equipped with scour protection and resting on soft substrate, even those that were tagged and released at over 9 km away from this location. This highlights the strong site fidelity of the species for certain areas and suggests that habitats found within the close vicinity of the monopile are suitable for the species. Due to the lack of data on the species' abundance before and after the OWF installation, it is unclear whether this strong site fidelity reflects an attraction effect of the species for this artificial habitat. *Scyliorhinus canicula* is a scavenger and opportunistic predator that feeds on benthic species, such as crustaceans and small fish (Sims et al., 2006). This species adapts its diet according to food availability and season (Martinho et al., 2012; Papadopoulo et al., 2023; Wieczorek et al., 2018). Scour protection and monopiles of OWF induce colonisation from fixed organisms that attract other sessile species (crustaceans and molluscs) (Degraer et al., 2020). This phenomenon locally increases prey availability and improves feeding opportunities for predators (Bergström et al., 2013). As such, different species are attracted to and use scour protection of turbine monopile as a feeding and/or shelter habitat, such as the European lobster *Homarus gammarus* (Thatcher et al., 2023), *G. morhua* (Reubens et al., 2014) and *P. platessa* (Buyse et al., 2022, 2023b). *Scyliorhinus canicula* may also use this artificial habitat for feeding and benefit from the rocky armor as shelter opportunities to rest and hide from conspecifics and predators.

Interestingly, our study highlighted a different temporal use of this specific area between sexes with females being more likely to be present at night than during the day. As shown in other studies (Sims et al., 2001; Wearmouth et al., 2012), females may be less active and hide in crevices during the day, provided here by scour protection. This could account for the reduced number of detections during the day, as rocks form a physical barrier that prevents the tag's acoustic signal from reaching the receivers.

5. Conclusion

Our study investigated occupancy patterns of *S. canicula* within an OWF and showed that tagged individuals stayed and used habitats within the area throughout the study period. General seasonal observations in habitat use coincide with previous knowledge of the species' ecology with low occurrence in coastal waters during winter. The species displays high degree of site fidelity and seems to favour soft

substrate habitats within the OWF, on which only one of the 5 monitored monopiles was installed. This monopile is also equipped with scour protection, which may serve as both a refuge and a feeding area for *S. canicula*. Although our results do not seem to show major effects of OWF on the behaviour of *S. canicula*, OWFs are increasingly developing on coastal habitats which could, on a larger scale, lead to changes in the behaviour of certain species such as species that migrate during their life cycle (van Berkel et al., 2020).

The use of a dense network of receivers around the monopiles to estimate the precise position of individuals over time using models, such as the Yaps (Baktoft et al., 2017), would provide deeper insights on individual activity patterns around monopiles and scour protection (Reubens et al., 2013b; Thatcher et al., 2023). Further investigations using fine-scale positioning are also required to evaluate the potential effect of EMF emitted by underwater cable on the occupancy patterns of *S. canicula*, and more generally benthic elasmobranch species, within OWF. Overall, this study contributes to improved ecological knowledge of *S. canicula* and provide original insights on how the installation of anthropogenic structures may impact this species.

CRediT authorship contribution statement

Pierre Labourgade: Writing – original draft, Formal analysis. **Lydie I.E. Couturier:** Writing – review & editing, Writing – original draft, Conceptualization. **Jérôme Bourjea:** Writing – review & editing, Conceptualization. **Mathieu Woillez:** Writing – review & editing, Conceptualization. **Eric Feunteun:** Writing – review & editing, Conceptualization. **Jan T. Reubens:** Writing – review & editing, Conceptualization. **Thomas Trancart:** Writing – review & editing, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106802.

Data availability

Data will be made available on request.

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